

A REVISION OF THE SHORE-FLY GENUS *RHYSOPHORA* CRESSON
(DIPTERA: EPHYDRIDAE)

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Abstract.—The New World genus *Rhysophora* Cresson, now placed in the tribe Discomyzini (subfamily Discomyzinae), is revised. Four species, including *R. griseola* (type locality: Costa Rica. Guanacaste: Colorado), which is newly described, are included. The phylogenetic relationships of the species of *Rhysophora* are reanalyzed, and brief comments are provided on the relationships of the genus within the tribe. A key to the genera of the tribe is included.

Key Words: Diptera, Ephydriidae, shore flies, *Rhysophora*, phylogeny

The subfamily Discomyzinae, presently comprising two tribes, 22 genera, and nearly 200 species (Zatwarnicki 1992, Mathis and Zatwarnicki, in preparation), is one of the smaller subfamilies of shore flies. One of the tribes, Discomyzini, with half of the genera (11) but only one-fourth of the species (ca. 50), includes the genus *Rhysophora* Cresson, the subject of this revision.

Cresson (1924) described *Rhysophora* as a monotypic genus with *R. robusta* Cresson as its type species. Cresson (1946) later transferred two previously described species, *Psilopa umbrosa* Loew and *P. caeruleiventris* Loew, to *Rhysophora*. Mathis and Wirth (1977), however, placed the latter two species in *Nesopsilopa* Mathis and Wirth, which is now recognized as a subgenus of *Guttipsilopa* Wirth (Mathis and Zatwarnicki 1990). Since the original description of *Rhysophora*, most references to the genus have been part of generalized studies, such as keys to genera (Cresson 1942, Sturtevant and Wheeler 1954, Wirth and Stone 1956) or regional catalogs (Wirth 1965, 1968). An exception is Mathis' (1977) revision of the genus, which included two new species, *R. ardeoceras* and *R. liropus*, and provided the

first phylogeny for the species. Mathis' phylogenetic analysis resulted in two basal lineages that were recognized as species groups: the *ardeoceras* group (*R. ardeoceras*) and the *robusta* group (*R. robusta* and *R. liropus*) as sister groups. A sister group to *Rhysophora* was not identified.

The phylogenetic relationships *Rhysophora* has with related genera within Discomyzini remain largely unresolved, although Zatwarnicki (in litt.) is now investigating them. Previously, Zatwarnicki (1992) accorded subfamilial status to Discomyzinae and reconstituted the two included tribes with *Rhysophora* and 10 other genera being moved from Psilopini to Discomyzini.

Information on the natural history and distribution of *Rhysophora* is meager. Adults are collected infrequently, resulting in a paucity of specimens and locality records. Some species are associated with plants of the family Pontederiaceae, perhaps as herbivores. Virtually nothing is known about the larval stages, behavior, or life history of *Rhysophora*. The species of *Rhysophora* are known thus far only from the New World.

The purpose of this study is to revise the

species, including the description of a new species, and to reanalyze the phylogeny of the species. We also discuss, albeit briefly, the position of *Rhysophora* within the tribe Discomyzini.

Methods.—The descriptive terminology, with the exceptions noted in Mathis (1986) and below, follows that published in the *Manual of Nearctic Diptera* (McAlpine 1981). The species descriptions are composite and not based solely on the holotypes. We have discovered or reinterpreted a majority of the characters used in this study, especially those from the male post-abdomen, and for that reason we are providing descriptions of all species. Four head and two venational ratios used in the descriptions are defined below (all ratios are averages of three specimens (the largest, smallest, and one other), except *R. ardeoceras* for which two specimens were measured):

1. Frons width-to-length ratio is the frons width divided by the frons length. The length is measured from the anterior margin of the frons to the posterior margin of the posterior ocelli. Width is measured at the level of the anterior ocellus.
2. Face width-to-height ratio is the narrowest width between the eyes divided by the height.
3. Gena-to-Eye ratio is the genal height measured at the maximum eye height divided by the eye height. In previous publications, this ratio was designated as the "eye-to-cheek ratio."
4. Eye width-to-height ratio is the eye width divided by the eye height, where both measurements are the longest distances taken with the eye oriented laterally.
5. Costal vein ratio is the straight line distance between the apices of R_{2+3} and R_{4+5} divided by the distance between the apices of R_1 and R_{2+3} .
6. M vein ratio is the straight line distance along M between crossvein dm-cu and

r-m divided by the distance apicad of crossvein dm-cu.

The phylogenetic analysis was performed with the assistance of Hennig86 (Farris 1988), a computerized algorithm that produces cladograms by parsimony. Before analysis, character data were arranged in transformation series and then polarized, primarily using outgroup procedures.

Terminology for structures of the male terminalia are provided directly on the illustrations of *R. ardeoceras* and *R. griseola* (Figs. 22–25, 30–33). Note that the term "postgonite," as used in Mathis (1993), is changed to "clasper," as in Zatwarnicki (1992) and Mathis (1994). This structure is part of the surstylur complex. The terminology is not repeated for comparable illustrations of other species.

Although most specimens for this study, including the primary types, are in the National Museum of Natural History (USNM), additional specimens were borrowed and studied from the Academy of Natural Sciences of Philadelphia (ANSP), Pennsylvania (Dr. Jon K. Gelhaus, Mr. Don Azuma); American Museum of Natural History (AMNH), New York, New York (Dr. David A. Grimaldi); Canadian National Collection (CNC), Ottawa, Canada (Dr. J. E. O'Hara, Mr. Bruce Cooper); University of Guelph (GUE), Guelph, Ontario, Canada (Dr. S. L. Marshall).

ANNOTATED KEY TO GENERA OF THE TRIBE DISCOMYZINI

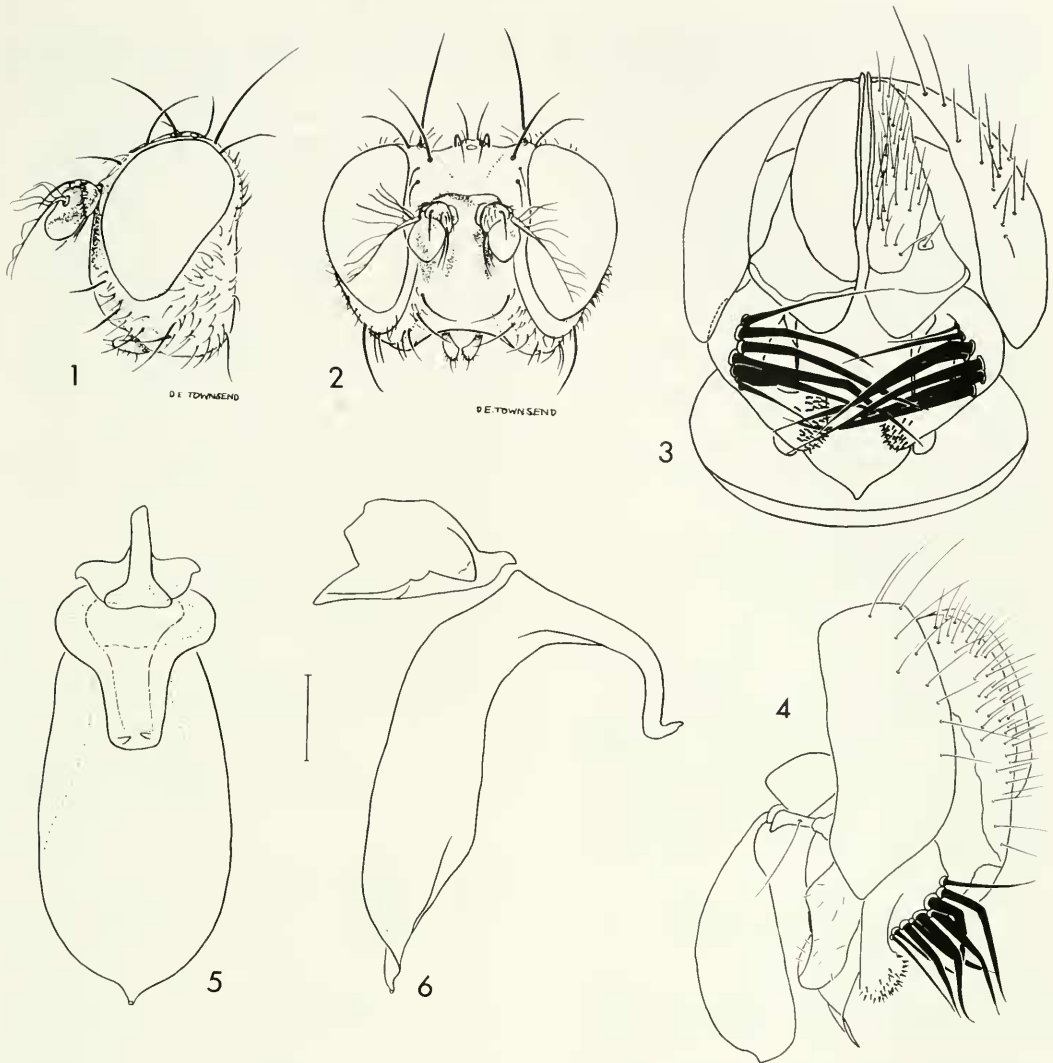
1. Wing spotted, usually white or hyaline spots on a dark background 2
 - Wing hyaline or with anterior margin darkened but not spotted 5
2. Supra-alar setae absent
 - *Trypetomima* de Meijere
[4 species; Old World (Australasian/
Oceanian and Oriental)]
 - Supra-alar seta present, size of seta moderate to well developed 3
3. Facial setae 2, dorsal seta well developed; arista bearing 7–8 dorsal rays; tibia or tarsus generally lighter colored than femur 4

- Facial setae 4, all well developed; arista bearing 14-16 dorsal rays; legs unicolorous, usually dark *Actocetor* Becker [1 species; Old World (Afrotropical and Oriental)]
- 4. Vein R_{2+3} basad of crossvein r-m bearing 3-4 black setulae; tibiae yellowish white with brown bands *Eremomusca* Mathis [1 species; *E. nussbaumi* Mathis 1985; Old World (Palearctic); Mathis 1985]
- Vein R_{2+3} basad of crossvein r-m bare; tibiae blackish brown, tarsi yellow with apical tarsomere dark *Guttipisilopa* Wirth (subgenus *Guttipisilopa*) [1 species; *G. (G.) haydeni* Wirth 1956; New World (Neotropical)]
- 5. Alula well developed 6
- Alula weakly developed, very narrow 9
- 6. Intrafrontal seta present; fronto-orbital setae 4 (anterior 2 setae proclinate, 3rd laterocline, 4th laterorecline) ... *Paratissa* Coquillett [4 species; Old and New Worlds (Afrotropical, Australasian/Oceanian, and Neotropical); Mathis 1993]
- Intrafrontal seta absent; fronto-orbital setae 2-3 7
- 7. Arista bearing 9-10 dorsal branches; supra-alar seta well developed, length subequal to postalar seta *Rhysophora* Cresson [4 species; New World (Nearctic and Neotropical)]
- Arista bearing 3-5 dorsal branches, rarely 6; supra-alar seta moderately well developed, length about half postalar seta 8
- 8. Vein R_{2+3} basad of crossvein r-m bearing 3-4 black setulae; legs unicolorous; maxillary palpus brown *Hostis* Cresson [1 species; *H. guamensis* Cresson 1945; Old World (Afrotropical and Australasian/Oceanian); Mathis 1993]
- Vein R_{2+3} basad of crossvein r-m bare; legs dark with yellow tarsus, apical tarsomere dark; maxillary palpus usually pale colored *Guttipisilopa* Wirth (subgenus *Nesopsilopa* Mathis and Wirth) [5 species; New World (Nearctic and Neotropical); Mathis and Wirth 1977]
- 9. Supra-alar seta present; prescutellar acrostichal seta absent; presutural seta minute and poorly developed; katapisternal seta 1; facial setae 3 pairs, all small and poorly developed *Discomyza* Meigen [9 species; Old and New Worlds (Afrotropical, Australasian/Oceanian, Nearctic, and Palearctic)]
- Supra-alar seta greatly reduced or absent; prescutellar acrostichal seta present; presutural seta well developed; katapisternal setae 2, dorsal seta larger; facial setae 3 pairs, dorsal pair cruciate, ventral pair poorly developed 10
- 10. Legs dark with yellow tarsi, apical tarsomere dark; alula narrow and bearing long, fine setae along margin *Mimapsilopa* Cresson [5 species; New World (Nearctic and Neotropical); Lizarralde de Grosso 1982]
- Legs unicolorous; alula reduced or absent . . . 11
- 11. Arista bearing 6-7 dorsal rays; anepisternal setae 2, ventral seta slightly less than twice length of dorsal seta; femur setulose, setae in rows *Helaeomyia* Cresson [2 species; New World (Nearctic and Neotropical); Lizarralde de Grosso 1982]
- Arista bearing 8-10 dorsal rays; anepisternal setae 2, ventral seta more than twice the length of the dorsal seta; femur bearing 2-3 prominent setae near the apex *Clasiopella* Hendel [2 species; Old World (Afrotropical, Australasian/Oceanian, Oriental); 1 species introduced to New World (Nearctic and Neotropical); Mathis 1994]

Genus *Rhysophora* Cresson

Rhysophora Cresson, 1924: 159. Type species: *Rhysophora robusta* Cresson, 1924, monotypy.—Cresson, 1942: 105, 123 [key, review].—Sturtevant and Wheeler, 1954: 160 [key].—Wirth and Stone, 1956: 465 [key].—Wirth, 1965: 743 [Nearctic catalog].—Mathis, 1977: 921-945 [revision].

Diagnosis.—Specimens of *Rhysophora* are similar to those of *Guttipisilopa* and other genera of Discomyzini but can be differentiated by the following combination of characters: outer vertical seta usually half or less length of inner seta, but never equal; proclinate fronto-orbital setae 1-2, inserted anteriorly of median, reclinate seta; intrafrontal setae lacking; arista bearing 8-15 dorsal rays; face generally with prominent antennal grooves (antennal grooves in *R. ardeoceras* and *R. griseola* are very shallow); supra-alar seta well developed; wing generally hyaline or faintly infuscate; vein R_{2+3} lacking setulae basad of crossvein r-m; alula well developed; hind basitarsus of male slightly swollen, with a ventral groove that bears a row of angularly recurved, pale setae.



Figs. 1-6. *Rhysophora liropus*. 1, Head, lateral view. 2, Same, anterior view. 3, Male genitalia, posterior view. 4, Same, lateral view. 5, Aedeagus and aedeagal apodeme, dorsal view. 6, Same, lateral view. Scale = 0.1 mm.

Description.—Moderately small to moderately large shore flies, length 2.4 to 4.4 mm; usually blackish brown.

Head: Frons wider than long; mesofrons generally triangular, with base towards vertex and anterior angle at ptilinal suture; triangle shape and size variable among species; fronto-orbits and mesofrons concolorous; ocellar triangle slightly raised with ocelli forming equilateral or isosceles tri-

angle; pseudopostocellar setae inserted close together just posteromedial of posterior ocelli; ocellar setae proclinate, well developed, inserted wide apart just posterolaterad of anterior ocellus; ocellar setae greater than twice length of pseudopostocellar setae; 2 poorly developed, minute setulae inserted anteromedial of rear ocelli; intrafrontal setae lacking; inner vertical seta large, usually twice or more length of outer seta;

postocular setulae minute, inserted posterior of either vertical seta, extended along eye posterior margin; fronto-orbital setae 2–3, posterior seta reclinate, 1–2 proclinate setae inserted anterior of reclinate seta; median fronto-orbital seta often reduced or missing. Antenna oriented anterolaterad; pedicel sparsely setulose, bearing 4–6 smaller setae along ventral edge with 1 seta long, prominent; arista inserted on dorsal base of velvety appearing, macropubescent flagellomere 1. Face higher than wide; presence of antennal grooves and facial carina variable; face usually convex in profile, bearing 2–4 inclinate facial setae along lateral margin parallelling parafacials; facial setae inserted just below midfacial height; genal seta 1, prominent, inclinate; gena and postgena setulose; occipital setae small, running along occiput. Eye higher than wide; gena-to-eye ratio less than 0.25. Mouthparts small; maxillary palpus sparsely setulose.

Thorax: Generally unicolorous or lighter colored laterally; scutellum parabolic, slightly convex with disc setulose. Chaetotaxy as follows: prescutellar acrostichal seta inserted slightly anterior of larger, laterally displaced dorsocentral seta; postalar seta large, subequal in length to dorsocentral seta; supra-alar seta 1; apical scutellar setae 1; subapical scutellar setae weakly developed; basal scutellar seta 1; notopleural setae 2, both inserted at same level just dorsad of ventral notopleural crease; postpronotal seta 1; anepisternal setae along posterior margin 2, ventral seta longer; katepisternum lightly setulose, bearing 1 large katepisternal seta, usually curved upward. Legs setulose with small setae; mid femur bearing 1 prominent spinelike seta on posteroventral margin, located at apical $\frac{1}{3}$; tibia bearing 1 prominent spine at apex, especially prominent on mid leg; hind basitarsomere of male slightly swollen, bearing a row of distinctive, pale, recurved setae arising from ventral groove; coxa with 1 larger seta along anterior margin and a whorl of small setae, prominent on mid coxa. Wings usually hyaline to yellow-

ish brown; halter yellowish white; costal vein ratio variable; M vein ratio usually close to 1; costal margin near basicosta and tegula bearing 2 larger setae; subcostal margin lined with stout, black setae and indented at vein R_1 ; smaller, black setae along costal margin ended at vein R_{4+5} ; alula very narrow; vein R_{2+3} basad of crossvein r-m lacking setulae.

Abdomen: Usually dark brown to black, setulose; posterior tergites slightly larger; posterior and lateral margins of tergites usually bearing larger setae; 4th and 5th tergites sometimes bearing semierect, larger setae. Male terminalia: symmetrical; epandrium broadly U-shaped in posterior view, usually becoming wider subventrally in lateral view; cercus with ventral margin gradually merged with membrane; surstylus variable, greatly reduced or prominent, variously shaped depending on species; clasper with 1 or 2 processes, each longer than wide; pregonite small (could be the fused pre- and postgonites), usually closely associated with hypandrium, bearing 1–2 long setulae; aedeagal apodeme L-shaped to triangular in lateral view; aedeagus variously shaped, depending on species; hypandrium concave or very shallowly depressed, nearly flat.

Distribution.—The genus is known thus far only from the New World, with greater diversity in the tropics.

Natural history.—Two species, *R. liropus* and *R. robusta*, are associated with plants of the family Pontederiaceae, more commonly known as pickerel weed (species of the genus *Pontederia* L.) and anchored water hyacinth (species of the genus *Eichhornia* K. Kunth). These often abundant plants are sometimes considered weeds, and the phytophagous species of *Rhysophora* may offer some measure of biological control. Adult flies are often collected by sweeping species of Pontederiaceae.

Discussion.—Although *Rhysophora* is well characterized and its monophyly reasonably well established, we remain relatively ignorant about its phylogenetic relationships within the tribe Discomyzini. This

tribe, which was only recently recharacterized, has received inadequate attention from the standpoint of phylogenetics, and the available information on relationships is limited to recent revisionary studies that are of limited scope and that do not impinge directly on *Rhysophora* (Mathis 1993, 1994). Moreover, one of the only synapomorphies that may indicate a sister group for *Rhysophora* is ambiguous. The species of *Rhysophora*, like *Guttipsilopa*, lack setulae on the dorsum of vein R_{2+3} . This is apparently a secondary reversal of a synapomorphy for the tribe (Zatwarnicki 1992). Although this character may indicate a sister-group relationship between these two genera, the loss could also have arisen independently in each genus. Zatwarnicki (personal communication) is now investigating these and other issues germane to the phylogeny of Disco-myzini and Psilopini, and for the present we defer to his study and analysis. We did consult with Zatwarnicki (personal communication), who suggested, albeit provisionally, that we use *Helaeomyia* as an out-group.

Although the evidence for the monophyly of *Rhysophora* is rather compelling (see "Phylogenetic Considerations"), the included species, with the exception of *R. liropus* and *R. robusta*, are comparatively heterogeneous in external features. Casual observation could easily lead one to wonder if the species are indeed closely related, especially *R. ardeoceras*, which has many pleiomorphic external features and is quite similar to other taxa in the tribe.

KEY TO SPECIES OF *RHYSOPHORA* CRESSON

- 1. Antennal grooves and facial carina weakly differentiated, grooves very shallowly impressed; ventral margin of face nearly flat; face height-to-width ratio 0.64 to 0.70; mid femur bearing 2-4 setae, including 1 prominent spinelike seta on posteroventral margin near apical 1/3; clasper a single process 2
- Antennal grooves and facial carina between antenna distinct; ventral margin of face broadly and deeply emarginate; face height-to-width

- ratio 0.75 to 0.81; mid femur bearing 1 prominent spinelike setae on posteroventral margin about apical 1/3; clasper with 2 fingerlike processes, posterior process of clasper bearing a row of long, conspicuous setae along posterior margin 3
- 2. General coloration blackish brown, without whitish microtomentum; pseudopostocellar setae well developed; flagellomere 1 longer than wide, pointed apically; presutural seta present; costal vein ratio 0.58 to 0.65; surstylus small, a narrow, bandlike, transverse process *R. ardeoceras* Mathis
- General coloration blackish brown with whitish microtomentum; pseudopostocellar setae greatly reduced or absent; flagellomere 1 bluntly rounded; presutural seta absent; costal vein ratio 0.31 to 0.35; surstylus large, conspicuous in lateral view as a bootlike process *R. griseola*, new species
- 3. General coloration black; antennal grooves very deep and distinct; ventral portion of face rugose; flagellomere 1 black; gena-to-eye ratio 0.09 to 0.11; color of tarsi sexually dimorphic: ♂ tarsi black; ♀ mid and hind tarsi yellow, fore tarsus blackish *R. robusta* Cresson
- General coloration grayish tan; antennal grooves less well defined; ventral margin of face not rugose; flagellomere 1 yellowish orange; gena-to-eye ratio 0.20 to 0.21; tarsi of ♂ and ♀ concolorous, yellowish brown with apical tarsomere black *R. liropus* Mathis

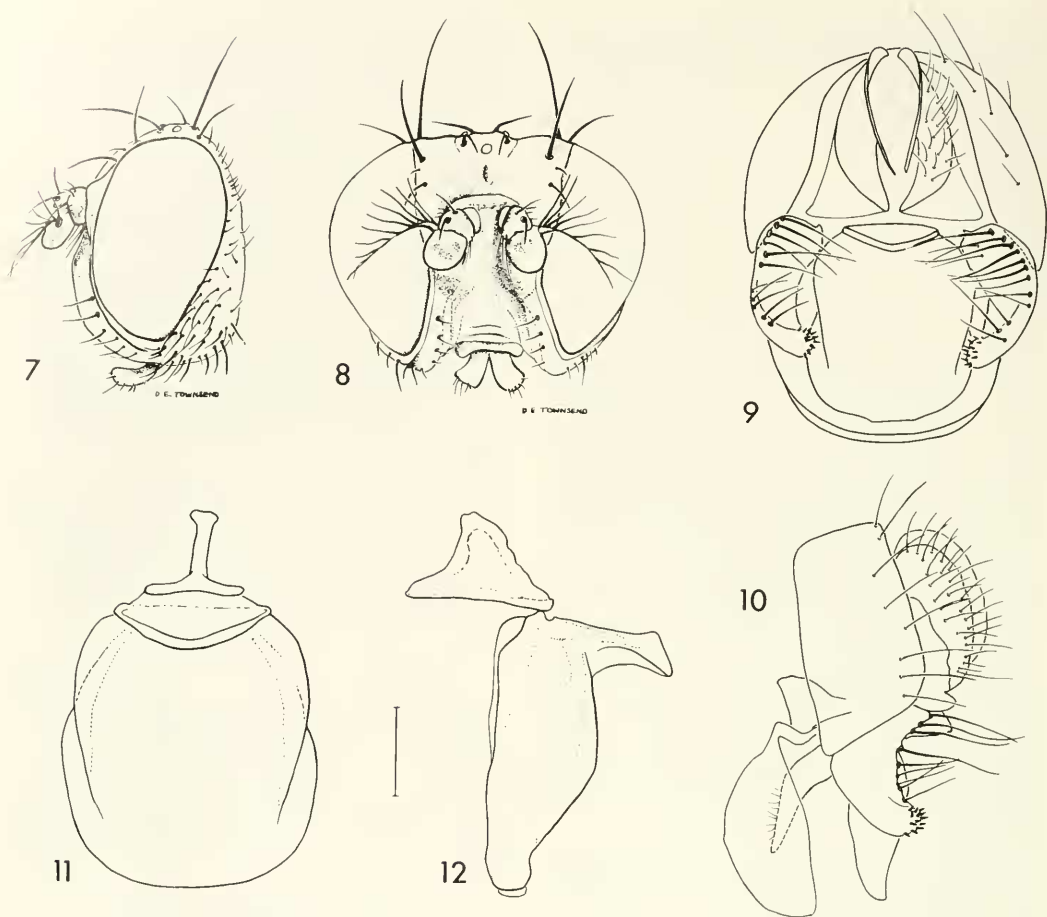
Rhysophora liropus Mathis
Figs. 1-6, 26

Rhysophora liropus Mathis, 1977: 931 [Argentina. Buenos Aires: Campana; HT ♂, USNM (75359)].

Diagnosis.—This species is closely related to *R. robusta* but can be distinguished by its generally grayish tan coloration; yellowish orange flagellomere 1; relatively smooth ventral margin of face, not rugose; wide gena (gena-to-eye ratio about 0.20); tarsi of ♂ and ♀ yellowish brown with apical tarsomere black.

Description.—Generally light gray to tan; medium-sized to moderately large sized shore flies, length 3.6-4.2 mm.

Head (Figs. 1-2): Frons width-to-length ratio 0.64-0.66; mesofrons rust brown, microtomentose, forming a lighter, raised pa-



Figs. 7-12. *Rhyssophora robusta*. 7, Head, lateral view. 8, Same, anterior view. 9, Male genitalia, posterior view. 10, Same, lateral view. 11, Aedeagus and aedeagal apodeme dorsal view. 12, Same, lateral view. Scale = 0.1 mm.

rabola with bluntly arched apex dorsal to parabolic ptilinal suture; frons between 2 raised portions slightly darker, depressed; inner vertical seta inserted close to outer seta, length of inner seta twice or more that of reduced outer seta; fronto-orbital plate narrow, slightly raised, wider at insertions of fronto-orbital setae; fronto-orbital setae 3; reclinate dorsal fronto-orbital seta approximately same length as ocellar setae; median seta slightly displaced laterally, proclinate and poorly developed; ventral fronto-orbital seta proclinate and twice length of median seta. Pedicel same color as frons but darker brown at base; pedicel bearing 2

setae, 1 proclinate spinelike seta on anterodorsal edge and 1 ventral seta slightly larger and better developed; flagellomere 1 yellowish orange with darker apex; flagellomere 1 short, subequal to combined length of scape and pedicel. Face width-to-height ratio 0.79-0.81; face golden gray and velvety; facial carina distinct; face emarginate and arched along ventral margin; lunule recedes inward to ptilinal suture at an angle; antennal grooves prominent but not deep; facial carina broad, not clearly defined; dorsal portion of face between antenna convex; face convex ventrally; parafacial crease clearly defined; facial setae 2-3, with 3-4

smaller setulae; minute setulae running along lateral margin of face parallel to parafacial; eye width-to-height ratio 0.71–0.73; gena-to-eye ratio 0.20–0.21; maxillary palpus brown, lighter ventrally.

Thorax: Greenish gray; dorsum with 4 dark brown lines faded anterior of transverse suture; 1 presutural seta; anepisternal setae 2; ventral seta twice as long as dorsal seta, both setae oriented slightly away from thorax. Femora and tibiae greenish gray, sometimes dark brown apically; tarsi light brown to yellowish with apical tarsomere darker brown to black; fore femur bearing 2–4 rows of long, fine setae on posterior margin. Wing brownish yellow; anterior margin relatively straight; costal vein ratio 0.61–0.63; M vein ratio 0.96–1.0; subcostal margin posterior to vein R_1 bearing 1 prominent seta; vein CuA_1 ends before fusing with margin. Halter brownish yellow.

Abdomen: Grayish green to grayish brown; anterior portion of tergites 3–5 brownish; 4th sternite of male completely sclerotized, lacking a membranous center. Male terminalia (Figs. 36) as follows: epandrium in lateral view becoming slightly wider ventrally with ventral margin broadly and bluntly rounded; cercus relatively long, occupying most of height of cercal cavity; surstylus greatly reduced, as a horizontal, narrow, bandlike process just ventrad of ventral margin of cerci; clasper well developed, deeply bifurcate a 2 fingerlike processes; posterior process of clasper (Figs. 3–4) narrowed medially, with linear dorsal lobe and spatulate ventral lobe, dorsal lobe bearing 8–10 robust, long setae along posterior margin, ventral lobe bearing numerous spine-like, short setae; anterior process of clasper (Fig. 4) nearly straight, relatively wide, with sub-basal enlargement on anterior margin, apex bluntly rounded, bearing numerous short setulae on anterior surface; aedeagal apodeme (Figs. 5–6) with extended keel rounded in lateral view; aedeagus (Figs. 5–6) about twice as long as wide, L-shaped in lateral view, with short, narrow, postero-

dorsal arm, larger arm narrowly rectangular in posterior view with apical margin shallowly mucronate; hypandrium concave, broadly rounded, wider than long, shallowly and narrowly emarginate at juncture with aedeagal apodeme.

Specimens examined.—ARGENTINA. Buenos Aires: Campana, Frente all astillero (on *Pontederia* as pupa), A-361, Nov 5 1973 (1 ♂; USNM); Dique Luján: Pupas de Dique Lujan (*Eichhornia azurea*), Acc. A-358c, 6 Nov 1973 (1 ♀; USNM).

Distribution (Fig. 26).—Neotropical: Argentina. Buenos Aires Province. This species is only known from the type series.

Natural history.—The allotype female was collected from anchored water hyacinth (*Eichhornia azurea* (Sw.) Kunth), and H. A. Cordo (in litt.) reared this species from a species of *Pontederia* in Argentina.

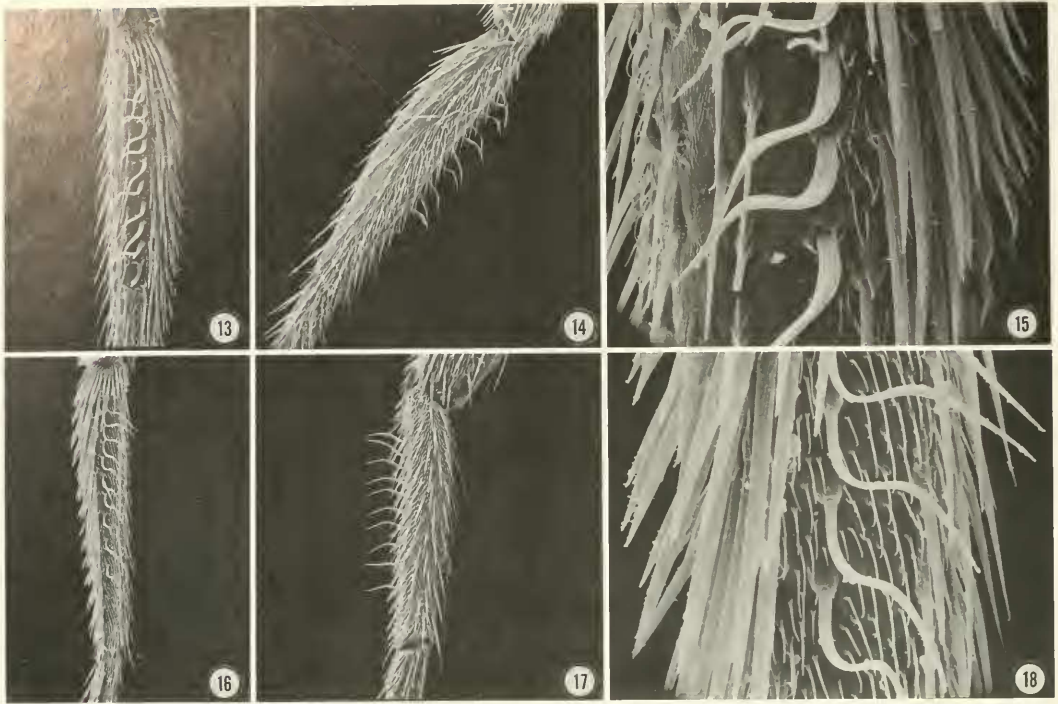
Rhysophora robusta Cresson

Figs. 7–15, 19

Rhysophora robusta Cresson, 1924: 159 [USA. Virginia: Fairfax Co., Dyke; HT ♂, USNM (56453)]; 1942: 123 [review].—Wirth, 1965: 743 [Nearctic catalog].—Mathis, 1977: 927–931 [revision].
Discocerina magna Coquillett in Johnson, 1910: 806 [nomen nudum].—Wirth, 1965: 743 [synonymy].

Diagnosis.—This species is closely related to *R. liropus* but can be differentiated by its generally black coloration, including flagellomere 1; rugose ventral portion of the face; short gena (gena-to-eye ratio about 0.10); and coloration of tarsi sexually dimorphic: ♂ black, ♀ with mid and hind legs yellow, foreleg black.

Description.—Generally black to brownish black; moderately small to moderately large shore flies, length 2.6–4.4 mm. Head (Figs. 7–8): Frons width-to-length ratio 0.48–0.59; frons black and indented ventrally; mesofrontal triangle lightly microtomentose with apex of triangle dorsad of ptilinal suture, ventral portion of triangle bearing a



Figs. 13–18. Scanning electron micrographs of *Rhysoptora robusta* and *R. ardeoceras*. 13, Hind basitarsus, ventral view. 14, Hind basitarsus, lateral view. 15, Hind basitarsus, enlargement of ventral view. *R. ardeoceras*: 16, Hind basitarsus, ventral view. 17, Hind basitarsus, lateral view. 18, Hind basitarsus, enlargement of ventral view.

slight indent; parafrons velvety, minutely microtomentose; pseudopostocellar seta well developed; inner vertical seta inserted close to outer seta, length of inner seta twice or more that of reduced outer seta; fronto-orbital plate narrow, slightly raised, wider at insertions of fronto-orbital setae; fronto-orbital setae 3, all inserted close together; large reclinate fronto-orbital seta inserted dorsally, about same length as outer vertical seta; proclinate fronto-orbital setae as large as pseudopostocellar seta; median fronto-orbital seta proclinate, often reduced or very minute; ventral seta proclinate. Pedicel black, bearing 2 prominent, spinelike, subequal setae on dorsal portion; posterior seta latero-clinate, anterior seta proclinate; arista bearing 9–10 long, dorsal rays; flagellomere 1 bluntly rounded at apex; flagellomere 1 as long as of slightly smaller than combined

length of scape and pedicel. Face width-to-height ratio 0.75–0.81; face black, similar to mesofrontal triangle; facial carina distinct; ventral margin of face broadly emarginate, arched and strongly rugose; lunule recedes inward almost horizontally to ptilinal suture; antennal grooves deep with a prominent, raised facial carina; face convex and velvety dorsal to facial carina; black parafacial crease divides velvety whitish parafacial from face; facial setae 4, inserted along lateral margin; 2–3 smaller, facial setae inserted anteriorly to 4 well-developed, inclinate facial setae. Eye width-to-height ratio 0.65–0.71; gena-to-eye ratio 0.09–0.11; maxillary palpus black.

Thorax: Generally black, unicolorous; presutural seta; anepisternal setae 2; dorsal seta less than $\frac{1}{2}$ length of ventral seta, 2–4 smaller setae inserted between and near these

2 seta. Legs black, concolorous; female mid and hind tarsi yellowish, with mid tarsus often brownish yellow; apical tarsomeres 1–3 of female blackish; male mid and hind tarsus black, sometimes lighter ventrally. Wings yellowish brown but darker dorsally; anterior margin relatively straight; costal vein ratio 0.58–0.62; M vein ratio 0.82–0.96; 1 stout spine along subcostal margin posterior to vein R_1 . Halter yellow.

Abdomen: Generally black, subshiny; 4th and 5th tergites lacking longer, dorso-oblique setae along posterior margin; 4th sternite of male completely sclerotized, lacking a membranous center. Male terminalia (Figs. 9–12) as follows: epandrium in lateral view becoming slightly wider ventrally with ventral margin broadly and bluntly rounded; cercus relatively long, occupying most of height of cercal cavity; surstylus greatly reduced, as a horizontal, narrow, bandlike process just ventrad of ventral margin of cerci; clasper well developed, deeply bifurcate as 2 fingerlike processes; posterior process of clasper (Figs. 9–10) somewhat L-shaped, anterior margin angulate in lateral view, posterior margin concave, rounded in lateral view, bearing numerous, long setae in row along concave, posterior margin, ventral apex broadly rounded, bearing numerous, short, spine-like setae apically; anterior process of clasper (Fig. 10) slightly angulate to curved and tapered gradually to apex in lateral view, in posterior view digitiform, broadly rounded, parallel sided, bearing numerous, short setulae along anterior surface; aedeagal apodeme (Figs. 11–12) triangular in lateral view; aedeagus (Figs. 11–12) longer than wide, L-shaped in lateral view, with posterodorsal arm shorter, roundly rectangular in posterior view with apical margin shallowly and broadly rounded; hypandrium concave, broadly rounded, wider than long, shallowly and widely emarginate at juncture with aedeagal apodeme.

Specimens examined.—CANADA. Ontario: Algonquin Park, 28 Jul, J. Mc-

Dunnough (3 ♂, 3 ♀; CNC, ANSP); Eagle Lake (*Pontederia*), 21 Jul 1976, S. L. Miller (1 ♂; GUE); Elgin, Hart Creek (*Pontederia*), 14–21 Jul 1977, S. L. Miller (1 ♂, 4 ♀; GUE); Lake Opinicon (*Pontederia*), 26 Jun 1977, S. L. Miller (1 ♂; QUE); Ottawa, 1 Jul 1958, A. L. Melander (4 ♂; ANSP, USNM); Sparrow Lake (*Pontederia*), 19 Jul 1976, S. L. Miller (1 ♂; GUE). Quebec: Lac Bernard, 7 Aug 1938, G. E. Shewell (1 ♂, 1 ♀; CNC); Perkins Mills, 14 Aug 1938, G. E. Shewell (6 ♂, 3 ♀; CNC); St. Pierre de Wakefield (on flowers of *Pontederia cordata* L.), 28 Jul 1961, J. R. Vockeroth (8 ♂, 10 ♀; CNC, USNM). UNITED STATES. Connecticut: Fairfield Co., Redding, 16–23 Jul 1930, 1932, A. L. Melander (4 ♂, 4 ♀; ANSP, USNM). District of Columbia: Anolston Island (Theodore Roosevelt Island), Laittle River (flowers of *Pontederia cordata*), 15 Jul 1916, H. L. Viereck (1 ♀; USNM). Florida: Dade Co., Royal Palm Park, 12–18 Apr 1923 (1 ♂; AMNH). Highlands Co., Archbold Biological Station (8 km W), 15 Apr 1989, W. & D. Mathis (11 ♂, 10 ♀; USNM); Highlands Hammock State Park, 20 Mar 1954, H. V. Weems, Jr. (1 ♀; USNM); Venus, 4 May 1961, H. V. Weems, (1 ♀; USNM). Marion Co., 10 May 1956, H. V. Weems Jr. (1 ♀; USNM). Putnam Co., Crescent City, 20 Apr 1908, VanDuzee (1 ♀; AMNH). Maine: Hancock Co., Bar Harbor, 5 Jul 1930, C. W. Johnson (1 ♂; USNM). Maryland: Prince Georges Co., Hyattsville, 1 Sep 1912, F. Knab, J. R. Malloch (1 ♂; USNM). Massachusetts: Barnstable Co., Pocasset, 26 Jul 1950, A. H. Sturtevant (2 ♂; USNM). Plymouth Co., Rochester, 21 Jul 1950, A. H. Sturtevant (1 ♂; USNM). Michigan: Mecosta Co., 24 Jul 1946, R. R. Dreisbach (1 ♀; USNM). New Jersey: Burlington Co., Riverton, Aug 1917, C. W. Johnson (1 ♂; USNM). New Hampshire: Cheshire Co., Keene, 4 Aug 1956, A. H. Sturtevant (1 ♂, 2 ♀; USNM). New York: Richmond Co., Staten Island, 1923 (1 ♂; USNM). Suffolk Co., Long Island, Riverhead, 4–16 Jun 1951, Roy Latham (4 ♀; USNM); Long Island,

Calent, 2 Sep 1954, Roy Latham (1 ♀; USNM); Long Island, Montauk, 11 Sep 1954, Roy Latham (1 ♂; USNM). West Nyack, 11 Jul 1920 (1 ♂; ANSP). Texas: Bastrop Co., Bastrop, 11 May 1954, L. D. Beamer (1 ♂, 1 ♀; USNM). Virginia: Fairfax Co., Mt. Vernon, 27 Jun 1915, W. L. McAtee (1 ♂; USNM); Dyke Marsh, 16 Jul 1916, W. L. McAtee (2 ♀; ANSP, USNM); Alexandria, 29 Jun 1952, W. W. Wirth (1 ♀; USNM). New Kent Co., Lanexa at Chickahominy River, 9 Jun 1984, W. E. Steiner, J. E. Lowry, A. G. Gerberich, D. S. Bogar (3 ♂, 1 ♀; USNM).

Distribution (Fig. 19).—Nearctic: Canada (ON, QB), USA (CT, DC, FL, ME, MD, MA, MI, NH, NJ, NY, TX, VA).

Remarks.—The coloration of the tarsi in this species is sexually dimorphic, with the tarsi of males being dark colored, mostly blackish, whereas the mid and hind tarsi of females are mostly yellow.

Rhysophora ardeoceras Mathis

Figs. 16–18, 20–26

Rhysophora ardeoceras Mathis, 1977: 936 [Costa Rica. Guanacaste: Tilaran (14 km NE); HT ♂, USNM (75360)].

Diagnosis.—This species is similar to *R. griseola* but is distinguished by the generally blackish brown coloration; fronto-orbital setae 2 (2nd proclinate seta lacking); elongate and pointed flagellomere 1; well-developed presutural seta; and short vein R_{2+3} (costal vein ratio about 0.60).

Description.—Generally blackish brown; moderately small to medium-sized shore flies, body length 2.4–3.3 mm.

Head: Frons width-to-length ratio 0.50–0.55; frons black and slightly indented ventrally; mesofrontal triangle subshiny with slightly arched vertex at straight ptilinal suture; ventral portion of triangle near vertex slightly shallow and lightly indented; fronto-orbital plate wide and slightly raised above level of triangle; dorsal fronto-orbital plate wide and fused with base of triangle;

parafrons velvety and minutely microtomentose between triangle and fronto-orbital plate, gently inclined dorsally; paler along ventral portions, bearing minute setulae; inner vertical seta inserted close to outer seta, relatively long, about 3 times longer than outer seta; fronto-orbital setae 2–3, inserted moderately close together; larger dorsal fronto-orbital seta reclinate, slightly larger than ocellar seta; median seta reduced or absent; ventral fronto-orbital seta proclinate, less well developed, $\frac{1}{2}$ length of dorsal seta. Antenna oriented laterally; pedicel blackish brown with 2 prominent spinelike setae on dorsal surface; posterior seta small and slightly latero-clinate, $\frac{1}{2}$ the length of anterior seta; anterior seta slightly smaller than enlarged ventral seta, well developed and proclinate; black arista bearing 12–15 long dorsal rays; flagellomere 1 yellowish orange near base, darker along margins; apex very acutely rounded, almost pointed; flagellomere 1 nearly twice as long as combined pedicel and scape. Face width-to-height ratio 0.64–0.70; face black, lighter and velvety ventrally; face lightly emarginate along ventral margin; lunule receded inward to ptilinal suture at a slight angle; antennal grooves very reduced or absent; facial carina absent; face convex between antenna; face wide and convex centrally; whitish parafacials on either side of raised face sloping ventrad to eye; facial setae 3; dorsal seta well developed and cruciate; ventral pair small, reduced; line of minute setulae running dorsal to black parafacial margin; eye width-to-height ratio 0.71; gena-to-eye ratio 0.10–0.11; gena whitish and heavily setulose but darker near post gena; clypeus and clypeal membrane brown; brown maxillary palpus long and slender; mouthparts brownish but reddish brown and lighter ventrally.

Thorax: Generally subshiny, blackish brown; presutural setae 1, about $\frac{1}{2}$ the length of supra-alar seta; anepisternal setae 2; dorsal seta oriented along thorax, ventral seta about three times as large as dorsal seta.

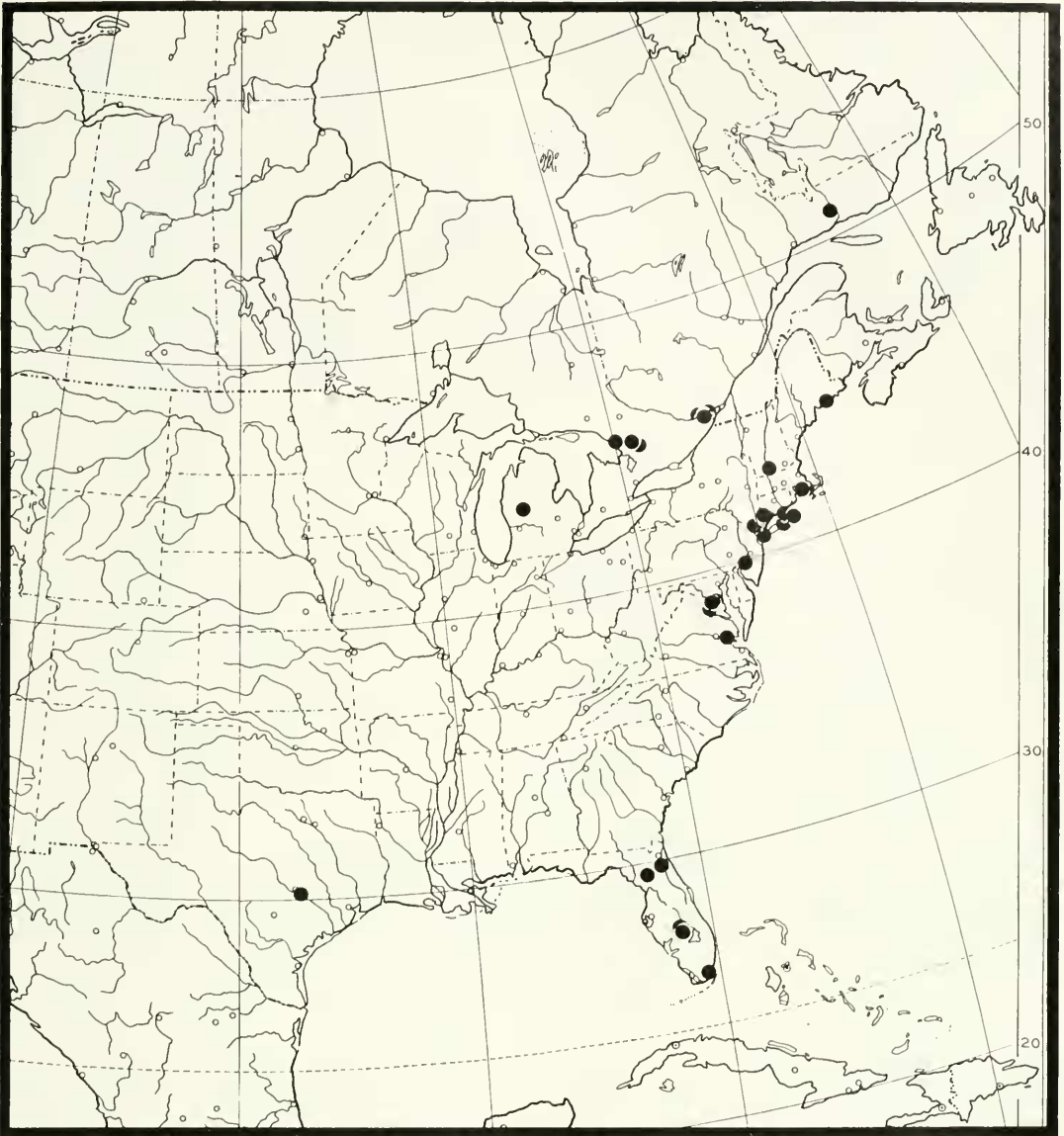
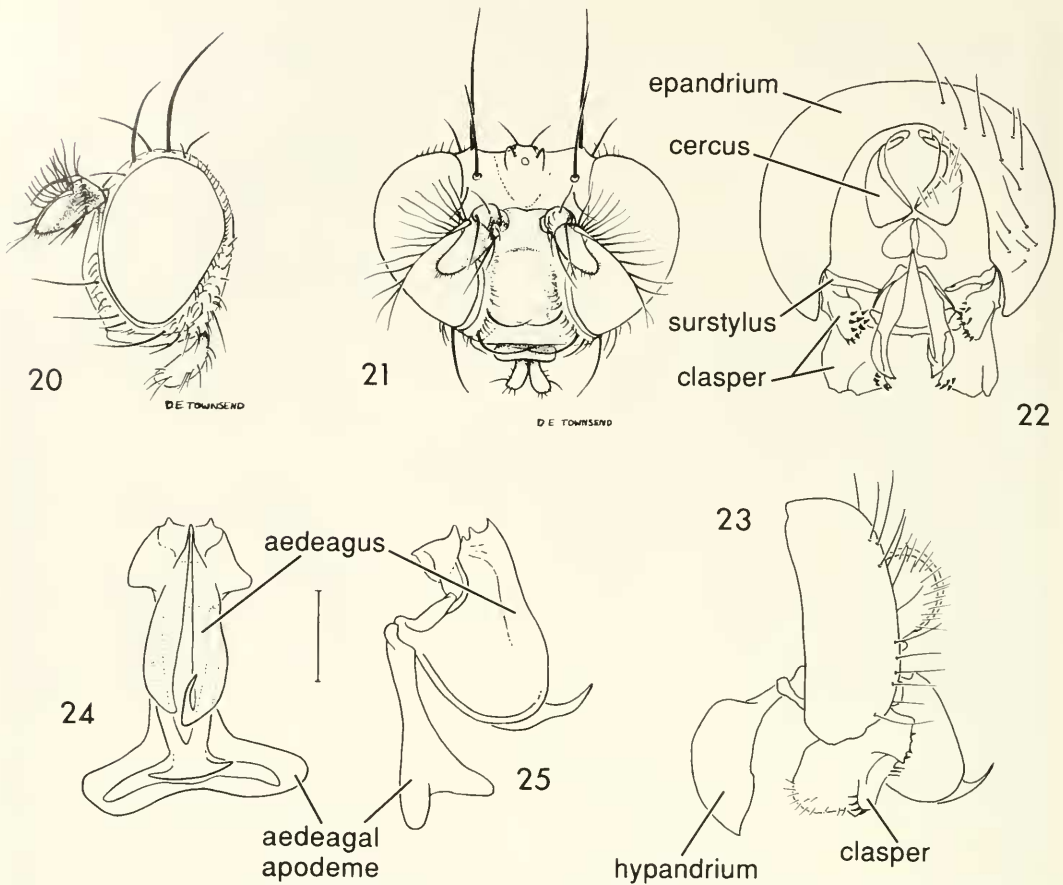


Fig. 19. Distribution map of *Rhyssophora robusta*.

Legs brownish black with yellowish tarsi; apical tarsomere blackish brown; mid femur bearing 3–4 prominent spinelike setae on posteroventral margin with 1 usually very well developed. Wings infumate and yellowish brown; costal vein ratio 0.58–0.65; M vein ratio 0.85–0.88; subcostal margin posterior to vein R_1 bearing 1 stout spine. Halter pale yellow.

Abdomen: Generally dark brown to black, subshiny; tergites 4 and 5 bearing several large dorso-obliquely oriented setae along posterior margin; 4th sternite of male with a membranous oval in center. Male terminalia (Figs. 22–25) as follows: epanandrium in lateral view parallel sided, slightly tapered on ventral $\frac{1}{4}$ to rounded ventral margin; cerci relatively short, occupying



Figs. 20–25. *Rhysophora ardeoceras*. 20, Head, lateral view. 21, Same, anterior view. 22, Male genitalia, posterior view. 23, Same, lateral view. 24, Aedeagus and aedeagal apodeme, dorsal view. 25, Same, lateral view. Scale = 0.1 mm.

about half height of cercal cavity; surstylus greatly reduced, horizontal, narrow, band-like process, situated just ventrad of cerci; clasper well developed (Figs. 22–23) relatively complex, bilobed with small cleft posteriorly, smaller dorsal lobe truncate posteriorly with posterior margin bearing numerous, short, spinelike setae; ventral lobe of clasper much larger, rounded anteriorly and ventrally, posterior margin truncate, with dorsal half bear several short, pale setulae in a comblike row, also bearing few setulae at posteroventral angle, especially along median surface; pregonite barlike, bearing 1 long seta, inserted medially; ae-

deagal apodeme (Figs. 24–25) relatively flat, lacking a conspicuous keel but with long lateral extensions; aedeagus (Figs. 24–25) tubular with dorsal slit, longer than wide, broadly rounded apically, with an apical, curved, narrow process oriented postero-ventrally, aedeagus in posterior view narrow, helmet shaped dorsally; hypandrium concave, broadly rounded, wider than long, shallowly and widely emarginate with a short projection at apex of each side of emargination, bearing a median, short keel along midline on internal surface.

Specimens examined.—COLOMBIA. Buenaventura, 2 Nov 1950, A. E. Michel-

bacher, E. S. Ross (2 ♂; USNM). COSTA RICA. Guanacaste: Tilaran (14 km NE), 5 Jun 1973, T. L. Erwin, G. H. Hevel (2 ♂, 1 ♀; USNM). EL SALVADOR. Santa Tecla (12 km NW; also known as Nueva San Salvador), Oct 1953, W. B. Heed (1 ♂; USNM). MEXICO. Jalisco: Barranquillas, 3 Feb 1964, E. I. Schlinger (1 ♀; USNM). Chiapas: Rio Izapa (near Tapachula), 21 Apr 1983, W. N. Mathis (1 ♂, 1 ♀; USNM). SURINAM. Paramaribo, Feb 1968, F. D. Bennett, H. Zwolfer (1 ♀; USNM).

Distribution (Fig. 26).—Neotropical: Suriname and Mexico (CHI, JAL, TEP) south through El Salvador and Costa Rica to Colombia.

Remarks.—Externally this species differs rather markedly from its congeners (see diagnosis and key). Despite its heterogeneity, it is apparently the sister group of the lineage giving rise to *R. liropus* and *R. robusta* (see "Phylogeny Considerations").

Rhysophora griseola Rao and Mathis,

NEW SPECIES

Figs. 26–33

Diagnosis.—Specimens of *R. griseola* are similar to those of *R. ardeoceras* but are distinguished by the generally blackish brown coloration with some whitish microtomentum; short and slightly rounded flagellomere 1; presutural seta lacking; and vein R_{2+3} long (costal vein ratio about 0.33).

Description.—Generally grayish black to black; medium-sized shore flies, length 3.3 to 3.9 mm.

Head: Frons width-to-length ratio 0.48–0.49; black frons deeply indented ventrally; mesofrons triangular, subshiny black with rounded vertex at crescent-shaped ptilinal suture; ventral portion of triangle near vertex shallow and indented; fronto-orbital plate wide and raised above mesofrons; dorsal portion of fronto-orbital plate wider, fused with base of mesofrons; parafrons appearing velvety and minutely microtomentose between mesofrons and fronto-orbital plate; pseudopostocellar seta greatly re-

duced or lacking (a pair of narrowly latero-proclinate setulae present, subequal in length to setulae within ocellar triangle); inner vertical seta inserted moderately close to outer vertical seta; outer vertical seta relatively long, about $\frac{2}{3}$ length of inner seta; fronto-orbital setae 3; reclinate fronto-orbital seta slightly shorter than outer vertical seta; median proclinate fronto-orbital seta minute and inserted slightly laterad; ventral proclinate fronto-orbital seta about $\frac{1}{2}$ length of reclinate seta. Antenna extended outward laterally; pedicel black with 2 prominent spinelike setae, posterior seta smaller, slightly latero-clinate, stronger anterior seta proclinate; arista black, bearing 8–10 dorsal rays; flagellomere 1 lighter along margins with apex bluntly rounded; flagellomere 1 slightly longer than combined length of scape and pedicel. Face width-to-height ratio 0.58–0.60; face with whitish microtomentum ventrally, dorsal areas near lunule and sometimes central areas blackish brown and microtomentose; ventral margin of face shallowly emarginate but mostly flat; lunule flat, receded inward to ptilinal suture at a slight angle; antennal groves very reduced or absent; facial carina absent; face slightly convex between antenna; face broadly convex centrally; white parafacials slanted ventrad, paralleling eye on either side of raised face, bearing setulae, becoming more densely, whitish microtomentose ventrally; facial setae 2–5, sometimes asymmetrical and displaced dorsally; eye width-to-height ratio 0.67–0.70; gena-to-eye ratio 0.11–0.15; gena with whitish microtomentose, especially along posterior margin; clypeus and clypeal membrane swollen; maxillary palpus blackish brown.

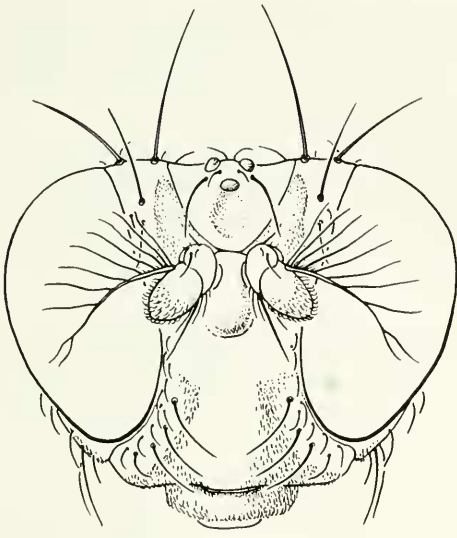
Thorax (Fig. 29): Blackish brown; scutellum with lighter triangular area, base at scutoscuteellar suture and vertex near scutellar apex; pleurae grayish and velvety; anepisternum, katepisternum, and parts of notopleuron covered by white microtomentum; presutural setae lacking; prescutellar acrostichal setae about half that of dorso-



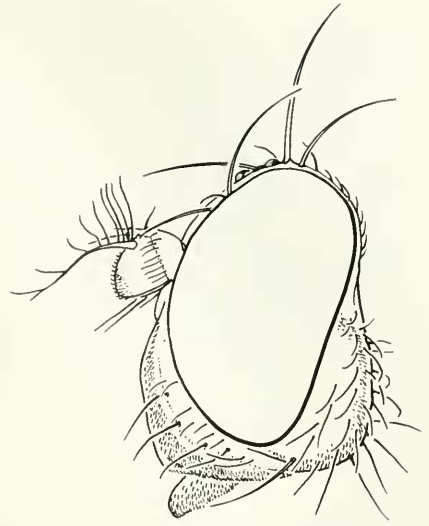
Fig. 26. Distribution map of *Rhysophora liropus* (diamond), *R. ardeoceras* (triangle), and *R. griseola* (dots).

central setae; notopleuron bearing 2 smaller, weakly developed setulae dorsally. Legs blackish brown; fore coxa with whitish microtomentum; microtomentum of fore femur and tibia lightly whitish; tarsi lighter,

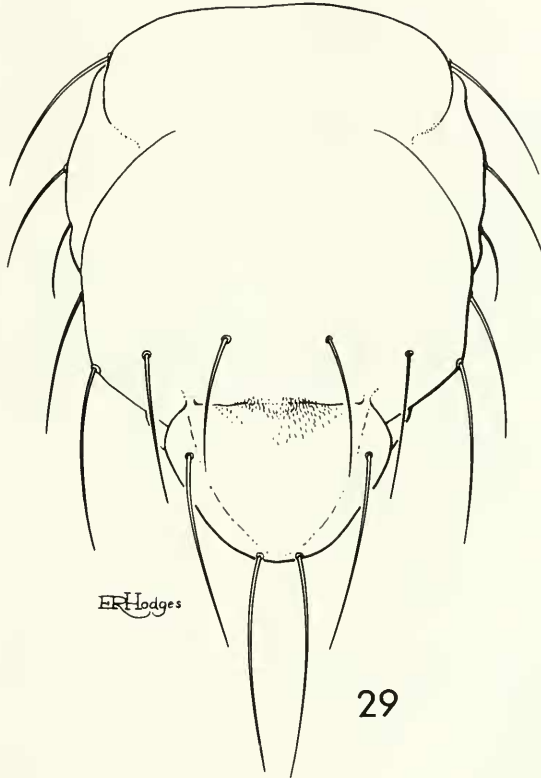
almost yellowish along ventral margin; mid femur bearing 3–6 prominent spinelike setae along posteroventral margin, usually with 1 seta enlarged. Wing with anterior margin relatively flat; yellowish brown and



27



28



29

Figs. 27-29. *Rhysophora griseola*. 27, Head, anterior view. 28, Same, lateral view. 29, Thorax, dorsal view. Scale = 0.5 mm.

slightly darker dorsally; halter white; costal vein ratio 0.31–0.35; M vein ratio 0.94–0.98; vein CuA₁ ends before margin.

Abdomen: Generally dark brown, subshiny; 4th sternite of male completely sclerotized, lacking a membranous center. Male terminalia (Figs. 30–33) as follows: epanthrium in lateral view becoming slightly wider subventrally, broadly and bluntly rounded ventrally, bearing a prominent seta along posterior margin just below midheight; cerci relatively long, occupying most of height of cercal cavity; surstylus well developed (Figs. 30–31) essentially bare of setae, shape angulate at about a right angle with ventral footlike portion enlarged and oriented posterolaterally, with a small, pointed tooth on mediodorsal surface; pregonite papillalike, bearing 2 long, apical setulae; clasper (Fig. 31) bare of setae, extended anteroventrally, tapered ventrally with apical $\frac{1}{3}$ enlarged, curved posteroventrally, and pointed apically; aedeagal apodeme (Figs. 32–33); aedeagus (Figs. 32–33) as wide as long, apical margin with 3 points, 2 lateral projections short, median point more prominent in posterior view; hypandrium very shallowly concave, appearing almost flat.

Type material.—The holotype male is labeled "COSTA RICA[,] Guanacaste Prov. Colorado[,] 31 March 1988/W. E. Steiner[,] J. M. Hill[,] J. M. Swearingen[,] J. M. Mitchell/HOLOTYPE ♂ *Rhysophora griseola* Rao & Mathis USNM [red; species name and gender symbol handwritten]." The allotype female and 14 other paratypes (3 ♂, 11 ♀; USNM) bear the same label data as the holotype. Other paratypes are as follows: MEXICO. Chiapas: Rio Izapa (near Tapachula), 21 Apr 1983, W. N. Mathis (1 ♂, 1 ♀; USNM). The holotype is double mounted (paper triangle), is in good condition, and is deposited in the USNM.

Other specimens examined.—ECUADOR. H. A. Parrish, 1914 (2 ♀; USNM). VENEZUELA. Anzoategue: Bergantin swamp near creek (river rocks), 7 May 1988, S. A.

Marshall (2 ♂; GUE). Federal District: Caracas, 3 Sep 1942, D. A. Iriarte (1 ♀; USNM).

Distribution (Fig. 26).—Neotropical: Mexico (CHI) south through Costa Rica to Venezuela and Ecuador.

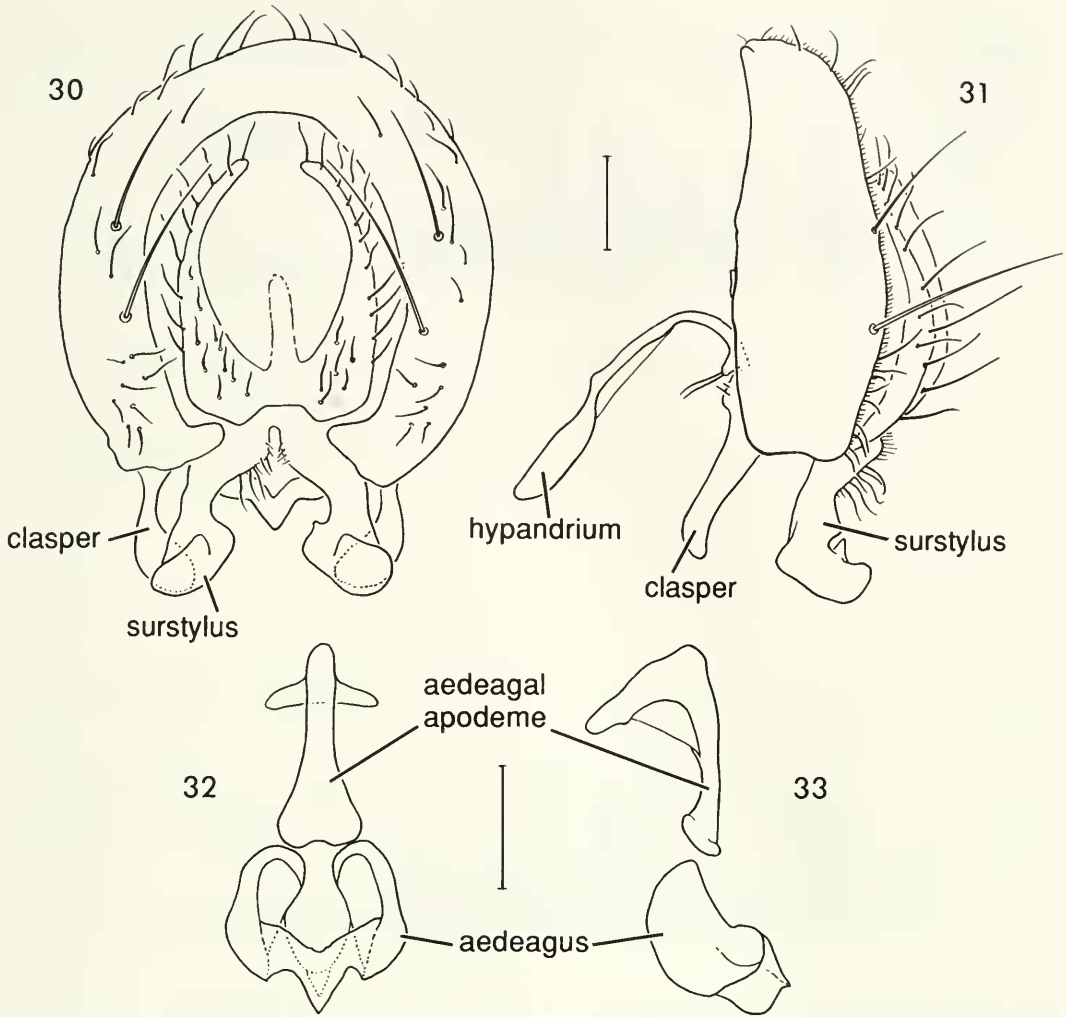
Etymology.—The specific epithet, *griseola*, is a Latinized adjective that refers to the whitish gray microtomentum, especially on the lateral margins of the face, post gena, and fore coxa.

Remarks.—This species is the basal lineage of *Rhysophora* according to the results of our phylogenetic analysis, differing from the remaining species in several characters.

PHYLOGENETIC CONSIDERATIONS

Rhysophora is one of 11 genera that comprise the tribe Discomyzini (Zatwarnicki 1992; *Clanoneurum* Becker, which was included in Discomyzini, has been returned to Psilopini (Zatwarnicki, personal communication)). Potential outgroups for phylogenetic analysis and the search for a sister group for *Rhysophora* were limited to the other 10 genera. We used four outgroups in the various analyses (*Guttipsilopa*, *Helaeomyia*, *Discomyza*, and *Mimapsilopa*,) and in the final analysis decided upon the former two, in part based on Zatwarnicki's recommendation (personal communication). These two genera are similar and probably closely related to *Rhysophora*. In our analysis, *Guttipsilopa* is indicated to be the sister group of *Rhysophora*, although that relationship must be considered tentative, as the only supportive synapomorphy is the secondary loss of setulae on vein R₂₊₃, which may be homoplasious. Regardless of the outgroup used, however, our analysis and the topology of the cladogram indicate that *Rhysophora* is monophyletic.

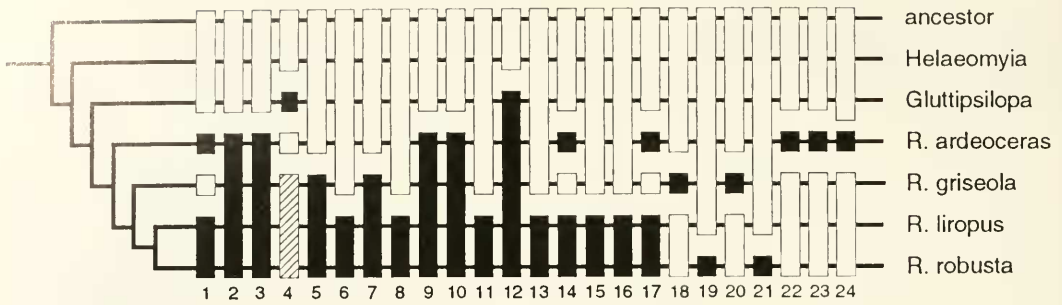
Before proceeding with the analysis of species relationships within *Rhysophora*, it is important to establish the monophyly of the genus. Unlike the unresolved sister-group relationships, the monophyly of *Rhysophora* is well established with synapo-



Figs. 30–33. *Rhysophora griseola*. 30, Male genitalia, posterior view. 31, Same, lateral view. 32, Aedeagus and aedeagal apodeme, dorsal view. 33, Same, lateral view. Scale = 0.1 mm.

morphies as follows: hind basitarsus slightly swollen; hind basitarsus of male with a ventral groove that bears a distinctive row of pale, recurved setulae; outer vertical seta shorter than inner seta, usually less than one-half the length of the latter (*R. griseola* is an exception, with the outer seta about $\frac{2}{3}$ the length of the inner seta); and pseudopostocellar setulae lateroreclinate. With the monophyly of *Rhysophora* established, we now focus on the phylogenetic relationships among the included species.

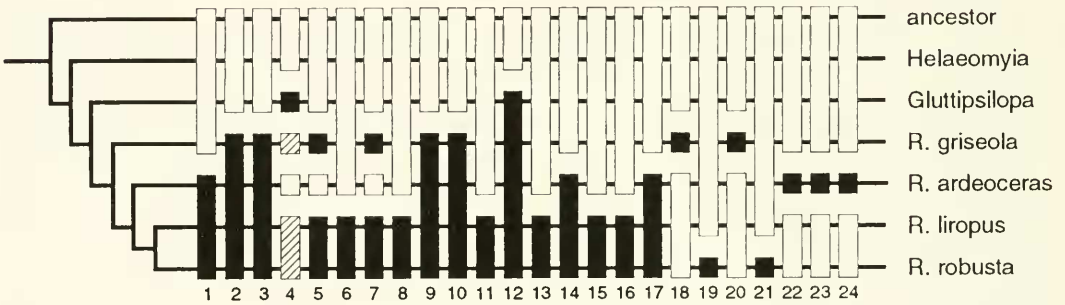
In the presentation on species relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion of its states or any qualifying comments. After the presentation of information on characters, an hypothesis of the cladistic relationships is presented and discussed. The cladograms (Figs. 34–35) are the primary mode for conveying these relationships; the discussion is a supplement to the cladogram and is intended only to complement the latter. In the



Length of 23 steps; Consistency Index 0.86; Retention Index 0.88.

Character:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Steps:	2	2	1	2	1	1	1	1	1	1	1	1	2	1	2	1	1	2
CI:	50	100	100	100	100	100	100	100	100	100	100	100	100	100	50	100	100	50
RI:	50	100	100	100	100	100	100	100	100	100	100	100	100	100	50	100	100	50

34



Length of 23 steps; Consistency Index 0.86; Retention Index 0.88.

Character:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Steps:	1	2	1	3	2	1	2	1	1	1	1	1	2	1	1	1	1
CI:	100	100	100	66	50	100	100	100	100	100	100	100	100	50	100	100	100
RI:	100	100	100	50	50	100	100	100	100	100	100	100	100	50	100	100	100

35

Figs. 34-35. Cladograms depicting hypothetical phylogenetic relationships among species of the genus *Rhyssophora* (with analysis and statistics of cladogram and characters). 34, With *R. griseola* as the sister group to *R. liropus* and *R. robusta*. 35, With *R. ardeoceras* as the sister group to *R. liropus* and *R. robusta*. CI = Consistency Index, RI = Retention Index.

discussion of character data, a "0" indicates the more plesiomorphic state (blank bars on the cladograms), with "1" (black bars on the cladogram) and "2" (hatched bars on the cladograms) indicating respectively more

derived states. The coding for nonadditive characters is reviewed on a character by character basis as indicated in the text. The numbers used in the presentation are the same as those on the cladogram (Fig. 34),

and the sequence is the same as noted in the character matrix (Table 1).

CHARACTERS USED IN THE
PHYLOGENETIC ANALYSIS

Head

1. Comparative lengths of inner and outer vertical setae: (0) vertical setae subequal in length, frequently with the outer seta slightly shorter; (1) outer vertical seta much shorter than inner seta, usually half or less. In most shore flies, including members of *Discomyzini*, the outer seta is slightly shorter than the inner seta, and the greatly reduced outer seta, as found in three of the species of *Rhysophora*, represents a synapomorphy.
2. Orientation of pseudopostocellar setae: (0) laterocline; (1) laterorecline; (2) lateroprocline. The more typical condition found in *Discomyzini* and *Psilopini* is for the pseudopostocellar setae to be reduced in length and widely latero-cline. In species of *Rhysophora*, these setae are usually well developed, and with a narrowly laterocline orientation. In specimens of *R. griseola* these setae are greatly reduced, with a slightly divergent, procline orientation, or lacking.
3. Shape of ptilinal suture: (0) somewhat flattened medially with curved lateral margins; (1) strongly arched, almost crescent shaped.
4. Shape of flagellomere 1: (0) apex narrowly pointed; (1) apex rounded; (2) apex bluntly rounded. The first flagellomere is generally conspicuously pointed, as found in *R. ardeoceras*. The rounded and bluntly rounded states are synapomorphies. Lacking an indication as to the transformation series for this character, we treated it as a nonadditive character.
5. Comparative lengths of flagellomere 1 and combined length of the scape and pedicel: (0) flagellomere 1 larger than the combined length of the scape and pedicel; (1) flagellomere 1 equal or slightly

Table 1. Matrix of characters and taxa used in the phylogenetic analysis (numbers for characters correspond with those used in text).

Taxa	Characters						
	1	2	3	4	5	6	7
Ancestor	0	0	0	0	0	0	0
<i>Helaeomyia</i>	0	0	0	0	1	0	0
<i>Guttipsilopa</i>	0	0	0	1	0	0	0
<i>R. ardeoceras</i>	1	1	0	0	1	0	1
<i>R. griseola</i>	0	2	1	0	1	0	0
<i>R. liropus</i>	1	1	1	1	1	1	1
<i>R. robusta</i>	1	1	1	1	1	1	1

shorter than the combined length of the scape and pedicel.

6. Antennal grooves and facial carina: (0) weakly developed or absent; (1) distinct, with relatively deep grooves and a well-defined carina. The generalized condition in the tribe is either a relatively flat face or with very shallow antennal grooves. The relatively deeply formed grooves of *R. liropus* and *R. robusta* are a synapomorphy.
7. Size and orientation of dorsal facial setae: (0) setae large, at least dorsalmost pair cruciate; (1) setae reduced in size, usually not cruciate. The generalized condition is for one, frequently the dorsalmost seta, or more of the facial setae to be cruciate. Although the facial setae in most species of *Rhysophora* are inclinate, they usually do not cross.
8. Shape of ventral facial margin: (0) nearly flat or very shallowly emarginate; (1) deeply emarginate.

Thorax

9. Row of distinctive, pale, curved setae inserted along anteroventral surface of male hind basitarsus: (0) setae absent; (1) setae present. This is a sexually dimorphic character and one of the primary synapomorphies to indicate the monophyly of the genus.
10. Size of male hind tarsus: (0) hind tarsus equal in size to mid and fore tarsi; (1)

hind tasu slightly swollen. Like the preceding character, this is a synapomorphy of the genus.

11. Spinelike setae along posteroventral margin of mid femur: (0) mid femur bearing 3–6 prominent setae; (1) mid femur bearing 1 prominent seta.
12. Setulae on dorsum of vein R_{2+3} basad of crossvein r-m: (0) setulae absent; (1) 3–4 setulae present; (2) setulae secondarily lost. The presence of setulae on the base of R_{2+3} is a synapomorphy for the tribe, and Zatwarnicki (1992) has interpreted their absence in *Rhyso-phora* and *Guttipsilopa* to be a secondary development.
13. Anterior wing margin: (0) shallowly arched, giving the overall appearance of a somewhat ovate wing; (1) somewhat flattened with anterior and posterior margins largely parallel.

Abdomen

14. Shape of surstylus: (0) well developed, although shape variable; (1) greatly reduced as a horizontal, narrow, bandlike process near the ventral margin of the cerci.
15. Shape of clasper: (0) simple, primarily a single process; (1) bifurcate, frequently deeply, resulting in 2 processes.
16. Setation of posterior process of the clasper: (0) a few setulae and at most a few setae present; (1) a row of long, conspicuous setae along posterior margin. The derived state is apparently unique to *R. liropus* and *R. robusta*.
17. Shape and setation of pregonite: (0) papillalike, bearing 2 long, apical setulae; (1) barlike, bearing 1 long seta, inserted medially.

AUTAPOMORPHIES NOT USED IN THE PHYLOGENETIC ANALYSIS

18. Development of pseudopostocellar setae: (0) pseudopostocellar setae well developed; (1) pseudopostocellar setae re-

duced and poorly developed. The derived state is unique to *R. griseola*.

19. Sculpturing of ventral portion of face: (0) similar to dorsal portions of face, generally relatively smooth; (1) rugose.
20. Presutural seta: (0) strongly developed; (1) seta absent. Most members of the tribe have a well developed presutural seta, and its apparent absence (or great reduction) in specimens of *R. griseola* is unique to that species.
21. Tarsal coloration: (0) males and females similarly colored; (1) sexually dimorphic, female mid and hind tarsi yellow, male mid and hind tarsi dark brown, concolorous with tarsus of foreleg.
22. Setae along posterior margin of tergites 4 & 5: (1) setae oriented along abdomen; (1) setae dorso-oblique.
23. Fourth male sternum: (0) 4th sternum entirely and evenly sclerotized; (1) 4th sternum with median, oval, membranous area.
24. Dorsal rays of arista: (0) 8–10 dorsal rays; (1) 12–15 dorsal rays.

Table 1 is the character matrix. From this matrix and using the implicit enumeration (ie) option of Hennig86, two trees (Fig. 34) of equal, "most parsimonious" length resulted (length of 23 steps, overall consistency index of 0.86, and a retention index of 0.88). Using the successive weighing technique (xsteps w, ie, cc), we further analyzed the characters to determine the goodness of fit for the two tree topologies. After successive weighing the same two trees resulted, and each character had a weight of 10. Other statistics of each character are cited with the cladograms (Figs. 34, 35).

The cladograms for the species of *Rhyso-phora* indicate that the genus is monophyletic (synapomorphies 2, 3, 9, 10, and 12). They also corroborate the monophyly of *R. robusta* and *R. liropus* (synapomorphies 6, 8, 11, 12, 13, 15, and 16), which was formerly recognized as a species group,

as a well-established monophyletic group that is the most derived lineage within the genus. Within the latter lineage, the species *R. robusta* is characterized by two autapomorphies (19, 21).

Our analysis indicates that the sister group giving rise to *R. liropus* and *R. robusta* is ambiguous, with either *R. ardeoceras* (synapomorphies 1, 14, 17), or *R. griseola* (synapomorphies 5, 7) being equal candidates. Of the two possibilities, we advocate *R. ardeoceras* (Fig. 34) as the better choice. The synapomorphies that demonstrate this relationship are based on structures of the male genitalia and are more reliable in our opinion than the shape of flagellomere 1, which is known to vary somewhat within the subfamily Discomyzinae. The species *R. ardeoceras* is distinguished by three autapomorphies (22, 23, and 24), and *R. griseola* is distinguished by two autapomorphies (18, 20).

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